The Evolution of Bourgeois, Parasitic, and Cooperative Reproductive Behaviors in Fishes

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Among vertebrate classes, fishes exhibit by far the greatest variability in competitive and cooperative behaviors in male reproduction. Scramble competition between reproductive males is one possibility. Another possibility occurs when resources, mates, or locations can be monopolized, in which case males may invest in primary access to fertilizations by adopting a "bourgeois" strategy, or they may employ alternative mating tactics to evade the reproductive monopoly of other males. Adaptations in morphology, physiology, and behavior to bourgeois and alternative phenotypes are highly divergent. Here I review the functional characteristics that differ between bourgeois and parasitic phenotypes, and discuss the variability of alternative reproductive tactics at the levels of plasticity, determination, and selection. Examples will illustrate the importance of ecology, and will suggest that variation in reproductive tactics is largely adaptive. Behavioral solutions to competition for mates and fertilizations often involve agonistic behavior and conflict, but also cooperation among competitors (e.g., when subordinate males pay a price to bourgeois males for gaining access to fertilizable eggs). Application of molecular genetic tools has helped to uncover intricate sexual and social relationships in various fish species, including species that display some of the most complex reproductive and social patterns known among the vertebrates.

Fishes are exceptional among vertebrates because of their unparalleled variability of reproductive and social patterns (Breder and Rosen 1966; Taborsky 1994, 1999). Male reproductive behavior, in particular, may be extremely diverse, both between and within species (for female alternative behaviors see Henson and Warner 1997). In principle, males may attempt to obtain access to fertilizable ova with any of four potential behavioral tactics: being quicker than rivals (scramble competition), monopolize resources (spawning sites, nests, all-purpose territories) or mates, exploit the monopolization of resources or mates by others (reproductive parasitism), or cooperate or "trade" with resource holders ("pay" for access by mutualism or reciprocity). The first of these possibilities works on a "first come, first go" basis, when resources, mates, or spawning locations are not economically defendable. However, even in group or broadcast spawners where this seems to apply, there may be subtle levels of monopolization that are not clear at a superficial look (Wedekind 1996). Unfortunately, hardly any data exist revealing the rules involved in such seemingly egalitarian reproductive activities in fishes. For this reason, I shall not discuss this possibility much further in this review.

The other three possibilities are characterized either by some sort of investment in primary access to mates or their gametes, or alternatively by exploiting such investment of others, or paying resource holders for the privilege of participation. The reason why these alternative reproductive tactics (ARTs) are so widespread in fish may be due to three features characteristic for this group (Taborsky 1999): (1) indeterminate growth, which results in a significant intrasexual size variation; (2) the prevalence of external fertilization, which makes it difficult to exclude sexual competitors by monopolization and allows simultaneous parasitic spawning (Taborsky 1984); and (3) the frequent occurrence of paternal investment (if brood care is shown at all), which raises the potential payoff to males who save this effort by employing a parasitic reproductive tactic. The first of these three causes appears to be by far the most important (Taborsky 1999).

In this article I review briefly how males specialize in either reproductive monopo-

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lization or parasitism, and how this relates to investment in morphologic, physiologic, and behavioral structures. Further, I discuss how ecology may influence variation in ARTs between individuals and populations of a species, and how cooperation of competitors may work as an alternative to conflict behavior. Finally, I illustrate with examples how the application of molecular genetics has helped us understand the coexistence of ARTs within a species.

Different Male Phenotypes

Males may either (1) invest in the primary access to mates or fertilizable eggs ("bourgeois tactic"), or (2) save this effort and attempt to evade the monopoly of resource holders ("parasitic tactic"; Taborsky 1997). Bourgeois males invest either in direct defense of mates, in monopolizing resources that are important to females, or in displaying traits that attract females because they signal male quality (such as courtship behavior or secondary sexual characters). Parasitic males exploit the reproductive investment of bourgeois males by behaving quickly (streaking) or inconspicuously (sneaking) to break the monopolization of mates by bourgeois males. Alternatively, such "secondary" males may provide something to the bourgeois males and thereby are permitted access to a portion of the fertilizable eggs (reproductive concession). Such mutualistic or reciprocal investment may include participation in duties like defense behavior or mate attraction (Fricke 1979; Lejeune 1985; Martin and Taborsky 1997; Santos 1985; Taborsky et al. 1987). This changes the relationship between these males from a pure bourgeois/parasite interaction toward a cooperative association (Taborsky 1994).

Reproductive competition may occur at either of two levels: for access to partners, or directly for fertilization of eggs at spawning. The bourgeois tactic typically involves the first level, where behavioral and morphologic adaptations are often subject to both intrasexual and intersexual selection. The parasitic tactic typically involves the second level, where special adaptations to competition are subject primarily to intrasexual selection (Taborsky 1999), though female avoidance of reproductive parasites may select also for inconspicuous characters (Henson and Warner 1997; Taborsky 1994).

Adaptations to Reproductive Monopolization

Behavioral investment in the primary access to mates by bourgeois males most often involves territory defense, which may serve to provision mates with shelters or food (Kuwamura 1986; Sato and Gashagaza 1997; Yanagisawa and Nishida 1991) or with a spawning site (McKaye et al. 1990; Rossiter and Yamagishi 1997). Sometimes a territory is used only as a starting point for spawning rushes into the water column, such as in many reef fishes that spawn in the pelagic environment (Warner 1987). In addition to defense, breeding substrate is often provided by bourgeois males, for example, in nest building species (Assem 1967; Potts 1984; Taborsky et al. 1987), or when snail shells serve for spawning and brood care (Sato 1994; Sato and Gashagaza 1997). Behavioral investment in mate attraction includes a great variety of courtship patterns that generally display the quality either of the courting male or of some resource that he provides (e.g., a nest or breeding shelter; Rowland 1984; Taborsky et al. 1987; Wirtz 1978; for an alternative hypothesis see Warner and Dill 2000).

Morphologic investment of bourgeois males includes the acquisition of large body size (Taborsky 1999) and the development of weapons that increase fighting potential, such as the kype or hooknose in salmon (Davidson 1935; Jones 1959; Tchernavin 1938). For the purpose of mate attraction, morphologic investment often involves decorations such as gaudy nuptial color patterns (Abel 1993; Bakker and Milinski 1993; Endler 1983) or specific body structures such as tubercles (Wedekind 1992) and sound producing organs (Brantley and Bass 1994).

Physiologic investment of bourgeois males is related to the production of hormones (Brantley et al. 1993) and possibly pheromones (de Jonge et al. 1989; see Taborsky 1999). Particularly the androgen 11-ketotestosterone appears to be important in the expression of secondary sex characters (Brantley et al. 1993). In some fish families, mucins are produced in special testicular glands, seminal vesicles, or hypertrophied kidneys (Bucher and Hofer 1993; Marconato et al. 1996; Nayyar and Sundararaj 1970; Rasotto 1995). These mucins may increase the viscosity of the seminal fluid, and they may prolong sperm longevity (Scaggiante et al. 1999) and serve to adhere sperm to the substrate on which eggs are deposited (Lahnsteiner et al. 1990; Marconato et al. 1996; Ota et al. 1996). Overall, from their reproductive effort bourgeois males may suffer an increased energy expenditure (Frischknecht 1993; Grantner and Taborsky 1998) that may reduce growth (Berghe 1992).

At the level of ejaculates and sperm, only a few adaptations of bourgeois males are yet known (Taborsky 1998). These include an increase in the amount of sperm per ejaculate with an increased potential of sperm competition (suggested by an interspecific comparison; Stockley et al. 1997), and a higher sperm concentration in bourgeois than in parasitic males (Atlantic salmon; Kazakov 1981).

Adaptations to Reproductive Parasitism

The adaptations to reproductive parasitism are usually contrary to those related to bourgeois tactics. On the behavioral level, for example, male reproductive parasites benefit from an inconspicuous performance, or from acting swiftly (Gross 1982; Taborsky et al. 1987). In fishes with internal fertilization, coercion is a tactic commonly adopted by inconspicuous males (Bisazza 1993). The major aim of parasitic males is to remain concealed to the males they wish to parasitize, or to avoid defensive actions in other ways, for example, by speed. The object is in effect to "scrounge by deception" (Barnard 1984). A specific example is that parasitic males may attain fertilizations by depositing sperm at the spawning site before eggs are laid (Kanoh 1996).

A morphologic feature that often increases the probability of success of parasitic males is small body size (Gross 1984), because small males are less conspicuous and may be more mobile and harder to pursue. Another important advantage to small males is that they may reproduce at an earlier age (Taborsky 1999). A second, frequent morphologic adaptation of parasitic males is a drab or camouflaged appearance (Gross 1982; Kodric-Brown 1986; Reeves 1907). Parasitic males may also benefit from mimicking females (Dominey 1981; see Taborsky 1994 for review). A common characteristic of all of these features of parasitic males is that they are "cheap," both energetically and with regard to mortality risk. Typically features displayed by bourgeois males to attract females are shunned, and thus it is equivocal whether the omission of investment by parasitic males should be viewed as morphologic "adaptations." In contrast, larger testis size is a clear morphologic adaptation of parasitic males that involves a strong energetic investment. Parasitic males typically have larger testes in relation to body size than their bourgeois conspecifics (Petersen and Warner 1998; Taborsky 1994). In only a few cases, however, has it been excluded that this is merely an effect of allometric growth (Gage et al. 1995; Taborsky 1998).

Allocation of energy toward sperm production is the major way that parasitic males can increase their fertilization probabilities by physiologic investment. As yet, a higher investment of parasitic males than bourgeois males in sperm production can be derived primarily from differences in testis size, as sperm production per se has not been measured and compared between these male tactics. In salmonids, stripped ejaculates suggested that in relation to body mass, parasitic males produced more sperm (Gage et al. 1995; Kazakov 1981; Linhart 1984), despite demonstrated higher sperm concentrations in ejaculates of bourgeois males (in Atlantic salmon; Kazakov 1981). Increased sperm production by parasitic males may coincide with the development of special sperm storage organs (seminal vesicles; Mazzoldi et al. 2000; Scaggiante et al. 1999). The production of androgens also appears to differ systematically between parasitic and bourgeois males (Brantley et al. 1993; Moore 1991; Stuart-Kregor et al. 1981).

Energy expenditure toward behavioral features, morphology, and physiology might seem to entail much higher costs in bourgeois than in parasitic males, but this is not necessarily true. Reproductive investment of parasitic males may be as high as in their bourgeois conspecifics, but the type of investment differs. In the Mediterranean wrasse *Symphodus ocellatus,* for example, parasitic males lost on average more than 0.5% of their body weight per day during the reproductive season, and completely stopped growing during that period, just as bourgeois males did (Taborsky 1994). The energetic costs to the reproductive parasites apparently resulted mainly from gonadal investment.

Parasitic males are subject to sperm competition to a much higher degree than bourgeois males (Taborsky 1998). Whereas the latter may often spawn without interference of other males, reproductive parasites usually shed sperm concurrently with bourgeois males and often also with other parasites. Therefore parasitic males should not only invest more in spermatogenesis (Parker 1990), but they may benefit also from investing in the production of sperm that perform more efficiently than that of bourgeois males. This has been demonstrated in salmonids, where parasitic males' sperm were found to be more mobile (Gage et al. 1995; Kazakov 1981; Linhart 1984) and to live longer than bourgeois males' sperm (Gage et al. 1995). Changes in sperm motility may also occur during aging. However, this may be an effect of an age-dependent role differentiation of males (see DeFraipont et al. 1993).

Fixed or Flexible Strategies and the Importance of Ecology

Alternative reproductive tactics may be flexible or fixed for life, genetically or environmentally determined, and they may result in equal or unequal Darwinian fitnesses. I have argued previously that the origin of ARTs should be viewed at three separate levels: plasticity, determination, and selection (Taborsky 1998, 1999).

Plasticity

Most ARTs result from a conditional choice of reproductive behavior (Dominey 1984; Gross 1996; Taborsky 1994). The critical variables determining the optimal behavioral choice of a male include relative body size and condition, the intensity of intrasexual competition (which depends on the operational sex ratio and on the relative frequencies of ARTs in the population), local population density, the sequence of residence, and environmental conditions such as predation risk which may determine the relative costs of the tactic (Taborsky 1994, 1998, 1999).

Whereas males may switch opportunistically between bourgeois and parasitic behavior, there are many examples of an ontogenetic transition from parasitic to bourgeois tactics (Taborsky 1999). This is due to indeterminate growth and the functional importance of body size in intrasexual competition. Only large males can efficiently monopolize mates or fertilizations.

Alternatively, ARTs may be fixed for life, but surprisingly few examples are known to date in which this has been substantiated (e.g., *Lepomis macrochirus,* Dominey 1980; Gross 1984; *Lamprologus callipterus,* Taborsky M, unpublished data). Fixed reproductive genotypes may result from either a genetic polymorphism or an ontogenetic switch causing irreversible specialization in the bourgeois or parasitic pathway. The latter may depend on variation in growth patterns or birth dates (Gross 1996; Taborsky 1998; Thorpe 1986). Fixed and plastic tactics that change with age or condition may exist side by side within a species, as exemplified by *Symphodus ocellatus* (Alonzo et al. 2000; see below).

Determination

To date, a genetic basis of ARTs has been demonstrated only rarely (Taborsky 1999). Environmental determination has been described more often, but this is easier to document (Gross 1996; Taborsky 1994). In fact, genetic and environmental effects may usually be expected to act in concert. Evidence for this exists in Atlantic salmon (Dalley et al. 1983; Glebe and Saunders 1986; Lundqvist and Fridberg 1982; Thorpe et al. 1983) and in a West African cichlid (Martin and Taborsky 1997).

Selection

ARTs may be maintained by frequency-dependent selection, with average bourgeois and parasitic males displaying similar lifetime fitnesses at equilibrium (Gross 1991, 1996; Taborsky 1999). Alternatively, the existence of ARTs may reflect a variation in male quality, with males in inferior condition using tactics that make the best of their situation and may result in lower average lifetime fitness (Dunbar 1982; Hazel et al. 1990; Taborsky 1998). How can the tactics of inferiors persist if they have some genetic basis? Random or systematic variation of environmental quality may result in substantial variation in male quality. For example, growth conditions may differ with spatial or social conditions, or with time. In a seasonal species, late-born males may be significantly smaller when reproducing as 1-year-olds than their early born, 1-year-old conspecifics. Due to the paramount importance of size for male monopolization of females, the late-born, small males may simply make "the best of a bad situation" when parasitizing bourgeois males. In this scenario, small males still do better to parasitize than to compete with large males for privileged access to females. To my knowledge, it has not yet been modeled under which environmental circumstances such tactics would be maintained in a population.

Lifetime fitness data are hard to obtain, so clear evidence is scarce as to which of these selection regimes applies (Gross 1996). In the live-bearing swordtail *Xyphophorus nigrensis,* different alleles at a Y locus are responsible for male sizes that correlate with the adoption of bourgeois or parasitic mating tactics, and Ryan et al. (1992) estimated that lifetime fitnesses of small and large males do not differ. Similarly, in species where fast-growing males perform the parasitic tactic later in life, such males probably do not suffer from a lower than average lifetime fitness. In such cases, ARTs probably produce similar lifetime fitnesses and may be balanced by frequency-dependent selection. Such might be the case in salmon (Dalley et al. 1983; Metcalfe et al. 1988; Thorpe and Morgan 1978, 1980), where Gross (1996) proposed that the average fitness of reproductive parasites may even exceed that of bourgeois males. On the contrary, when environmentally determined size variation is great in a short-lived species whose bourgeois and parasitic males have little potential for mortality differences, it is likely that small males are making the best of a bad situation (e.g., Kodric-Brown 1986; but see Alonzo et al. 2000).

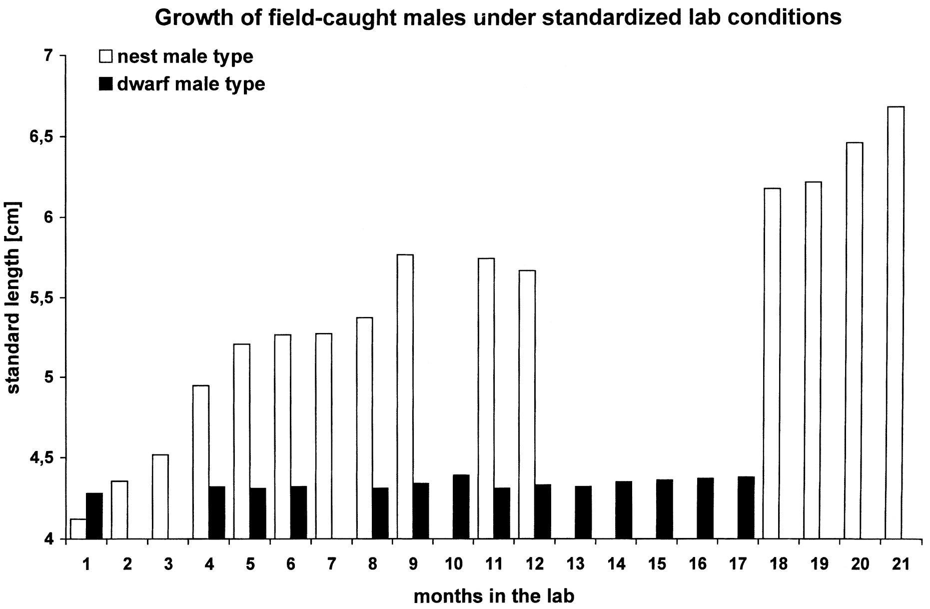

Figure 1. Growth of *L. callipterus* males belonging to nest male and dwarf male phenotypes. Fifteen males behaving as sneakers (nest male phenotype) and 19 males behaving as dwarf males were caught when active at Wonzye Point in March 1998 and 1999. After being transported to Vienna, they were kept in 160 L tanks under standardized conditions (see Schütz and Taborsky 2000), and weighed and measured at nearly monthly intervals. Data shown are arithmetic means of standard lengths.

An Example: *Lamprologus callipterus*

The complexity that may be involved at all three levels (plasticity, determination, and selection) and the importance of ecology for the evolution of ARTs may be illustrated with *Lamprologus callipterus,* a cichlid species breeding in empty gastropod shells. Large, bourgeois males of this species defend snail shell nests to which females are attracted (Sato 1994). The much smaller females (13 times less mass than bourgeois males on average; Schütz and Taborsky 2000) eventually spawn in a shell and remain in it for nearly 2 weeks to care for the eggs and larvae. Only the largest males in a population defend nests; they must pass a threshold size to carry shells (Schütz 1998). These bourgeois males can be extremely haremic (Sato and Gashagaza 1997). Medium-size males attempt to fertilize eggs parasitically when a nest owner is busy with defense, courtship, or shell collection. Dwarf males that are even smaller than females attempt to enter shells in which females are spawning. They squeeze themselves into the shell's aperture alongside the female, but have to wait until the female retreats a bit to pass her and settle at the tip of the shell (Taborsky 1998).

The parasitic tactic of medium-size males is opportunistic and transitional, that is, "plastic" and not fixed. All males that have passed female size continue to grow until they are large enough to carry shells, at which time they start to build and defend nests (Figure 1; Schütz 1998). We do not know whether all nest males have previously acted as sneakers, however. The situation is entirely different for dwarf males, which halt growth long before reaching female size (Figure 1). A dwarf male that has started to reproduce remains small and bound to the parasitic tactic throughout life.

This does not indicate whether the dwarf male tactic is genetically determined or whether these males stop growing in response to some environmental condition. A simple rule could be "if growth conditions are bad when approaching sexual maturity, invest in gonads instead of further growth." In a second step, these males could then halt growth entirely once they have become sexually mature at an early age. However, there is evidence that the dwarf male tactic is indeed genetically determined. Under standardized conditions in the laboratory, we raised one brood each of representatives of all three types of males that had been caught at the northern end of Lake Tanganyika. Although the offspring of sneaker and bourgeois males did not differ in growth, the offspring of dwarf males grew significantly slower, and more importantly, stopped growing completely before reaching female size (Figure 2). This experiment must be replicated, but these preliminary data indicate that two male genotypes may exist in this species: (1) a "nest male" type that performs reproductive parasitism in earlier stages of life, but finally reproduces as a bourgeois nest owner; and (2) a "dwarf male" type that halts growth after reaching sexual maturity and remains parasitic throughout its reproductive life. Further support for this conclusion comes from the fact that among many progeny of different nest males raised in the laboratory, we did not find any dwarf males (Schütz D, Pachler G, and Taborsky M, unpublished data).

If dwarf males in *L. callipterus* are a genetic morph, it is likely that this polymorphism is balanced by frequency-dependent selection, which means that over their lifetime both male types will on average produce similar numbers of surviving offspring. This is hard to demonstrate, but in principle molecular paternity analyses might help. Using microsatellite markers at four loci, we analyzed 442 young from 15 independent broods collected in the field. From a random sample of 10 broods from 10 different nests, paternity by the nest owner could be excluded in only two cases: in 1 of 27 young from one nest, and in all 19 young of another (Meidl 1999). For 92% of young, the respective nest owners were most likely the genetic sires (combined average exclusion probabilities for the loci were greater than 0.99). This suggests that nest owners are on average much more successful than dwarf males. However, if dwarf males can reproduce at least 1 year earlier than bourgeois males (Schütz D, unpublished data), then this might compensate the higher mean reproductive success of bourgeois males.

How does ecology affect the existence

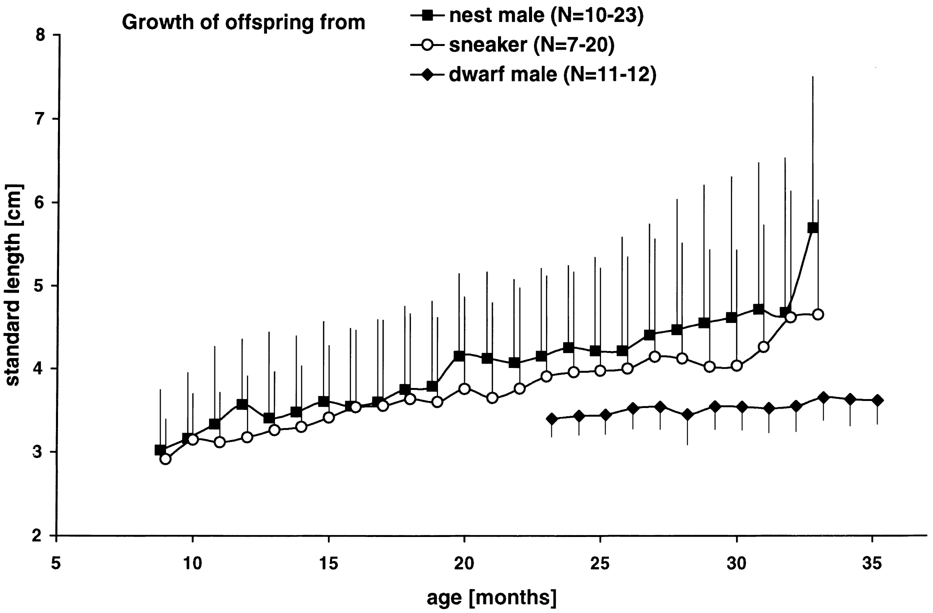

Figure 2. Growth of offspring from a nest male, a sneaker, and a dwarf male of *L. callipterus* caught at Kalundu. The first-generation offspring of these males were kept in 160 L tanks under standardized conditions (see Schütz and Taborsky 2000) and measured at monthly intervals for the periods shown in the graph. The numbers of offspring declined during this growth experiment due to mortality, from 23 to 10 in nest male offspring, from 20 to 7 in sneaker offspring, and from 12 to 11 in dwarf male offspring. Arithmetic means and standard deviations of standard lengths are given.

and frequency of different male reproductive tactics in *L. callipterus*? An experimental study suggested that the breeding substrate is important for the evolution of male and female sizes in this species (Schütz 1998; Schütz and Taborsky 2000). The availability and size of shells are probably important also for the mating pattern and for the evolution of alternative mating tactics. The shells of two different gastropod species are used for breeding by *L. callipterus.* Preferred shells are from *Neothauma tanganicense,* a large and locally abundant snail. The much smaller shells of the second species, *Paramelania damoni,* are used by *L. callipterus* in the northern part of Lake Tanganyika, where *N. tanganicense* is less abundant (Sato and Gashagaza 1997).

T. Sato investigated the reproductive ecology of *L. callipterus* at three locations spread between the northern and southern ends of Lake Tanganyika. Habitat and shell distribution differed greatly between these three locations (Table 1). At Kalundu, near the northern end, nest males are relatively large and highly haremic. Sneakers do occur, but dwarf males have not been found (Sato 1994). On the east coast at Rumonge, males are only half as big as in the northern population and there is little size variation between reproductively active males. Here the degree of polygyny is rather small, and there is no evidence for reproductive parasites (Sato and Gashagaza 1997). In a population close to the southern tip of the lake at Wonzye Point, the shell distribution is clumped, mainly because of the shell collection activity of *L. callipterus.* Here nest males reach very large body sizes, obtain large harems, and have to compete with two types of parasitic males: sneakers and dwarfs (Taborsky M, personal observation; see Table 1).

To understand the variation of the occurrence of male ARTs between populations, we must ask: (1) Why are there few or no parasitic males in the shell bed population at Rumonge? and (2) Why do dwarf males seem to occur only at Wonzye Point? At Rumonge, the substrate consists entirely of shells, so there is no need to collect shells for breeding. Therefore males can monopolize nests and breed when they are small. The optimal tactic is to grow rapidly and reproduce as a bourgeois male once a size has been reached that is sufficient to compete with other males. At Wonzye Point, however, males must grow much larger to build and defend a nest because a threshold size is needed to carry shells efficiently (Schütz 1998). In this case, it appears beneficial to begin reproduction earlier, that is, before the size of a nest male has been obtained, as few males will reach that final stage. It may be particularly desirable to reproduce as a dwarf, because at Wonzye Point *L. callipterus* breeds exclusively in large shells, which dwarf males can enter completely, providing them with an ideal position to fertilize eggs (Meidl 1999). In the northern Kalundu site, however, the large *Neothauma* shells are scarce, and for that reason dwarf males there would probably have a low success rate.

This example suggests that variation in an important ecological factor (the type,

Table 1. *L. callipterus* populations were surveyed at three locations spread out along the coast of Lake Tanganyika (Kalundu: northwest end of the lake; Rumonge: east coast; Wonzye Point: southern end of the lake)

			Mean number of shells per nest			Mating pattern		
						Number of females per nesting male		
Location	Habitat	Shell distribution	Small shells (*Paramelania damoni*)	Large shells (*Neothauma tanganicense*)	Mean male size (mm)	Mean	Maximum	Alternative tactics
Kalundu (Congo)	Sand slope	Low density	47	5	95	5.5	14	Sneakers (small and medium males)
Rumonge (Burundi)	Shell bed	Homogeneous and unlimited	—	high	47	2.4	7	None
Wonzye (Zambia)	Sand/rock margin	Clumped	—	96	116	4	18	Sneakers (small and medium males), dwarf parasitic males

Habitat and shell distribution was determined, standard lengths of nest males were measured, and the numbers of shells and females per nest were counted (Sato 1994; Sato and Gashagaza 1997; T. Sato, personal communication; the database at Wonzye Point was augmented by my own observations). The mean number of shells per nest at Rumonge was high but uncounted. The existence of alternative male tactics was surveyed by extensive underwater observations using SCUBA.

size, and abundance of breeding substrate) may strongly influence male body size, mating pattern (degree of polygyny), and the existence and form of ARTs.

Cooperative Behavior as a Competitive Strategy

Cooperation of competitors may work as an alternative to conflict behavior (Taborsky 1994). Competing individuals may cooperate or "trade" with resource holders, that is, they "pay" for access by mutualism or reciprocity (Taborsky 1999). In return, a bourgeois male may tolerate the presence and the activities of the cooperator to some extent, providing the latter with better fertilization possibilities (Fricke 1979; Kodric-Brown 1986; Ross 1983; Santos and Almada 1988; Taborsky et al. 1987). There are various ways in which bourgeois males can benefit from the presence of such "satellite males." Most often the latter share in defense of the territory (Fricke 1979; Lejeune 1985; Martin and Taborsky 1997), but they may also help in nest building (Reighard 1943; Wallin 1989) or in mate attraction (Fahy 1954; Hackney et al. 1967). Sometimes cooperative brood care may be present, either with an extended family structure (Balshine-Earn et al. 1998; Kohler 1998; Taborsky 1984, 1994; Taborsky and Limberger 1981) or with satellites that are accepted in a territory (Martin and Taborsky 1997). Other reasons for alloparental care (which I shall not deal with here) may occur in different contexts, such as when broods merge or nests are taken over (Taborsky 1994).

Here I shall briefly explain the two forms of cooperative behavior that at least to some extent appear to be adaptations to reproductive competition. These involve cooperation between (1) bourgeois and satellite males and (2) members of extended families. I shall illustrate these two pathways with four examples that have been studied in some detail.

Symphodus ocellatus

In the Mediterranean ocellated wrasse, satellite males help to defend the nest against small parasitic males (sneakers) that attempt to steal fertilizations by simultaneous parasitic spawning. Satellites are tolerated by the nest owners, and they stay at a particular nest for most of its spawning period (Taborsky et al. 1987). Afterward they leave to join another nest. Satellites benefit by improved access to fertilizable eggs (twice the spawning rate of sneakers; Taborsky M, Wirtz P, and Taborsky B, unpublished data), but do not share in brood care or in defense against egg predators. When satellites were removed from these territories and released at "their" nests again after a period of 20 min, the behavior and success of nest owners (agonistic behavior against conspecific males, courtship, brood care, spawning rate, and the number of parasitized spawnings) did not differ significantly between periods with and without satellites. However, nests with satellites received more female visits and more spawnings in the long run, and were much more successful. Thus 48 of 56 nests with satellites survived to hatching, whereas only 4 of 30 nests without satellites had any hatching success (Taborsky M, Wirtz P, and Taborsky B, unpublished data). Similar relationships between satellite and bourgeois males have been observed in the Azorean rock-pool blenny (*Parablennius sanguinolentus*; Santos 1985; Santos and Almada 1988), where nests with satellites also received more female visits and more spawnings, again suggesting a role in mate attraction for satellite males (Oliveira RF, Goncalves, EJ, and Santos, RS, unpublished data). In both species, it remains to be tested whether the presence of satellites is a cause or consequence of nest male success. Probably both elements of causation are involved, for example, by a positive feedback mechanism between a nest's attraction to satellites and females.

Satellites who remain in the vicinity of bourgeois males' spawning sites have also been observed in various species belonging to the families Cyprinidae, Cyprinodontidae, Cichlidae, Embiotocidae, Pomacentridae, Tetraodontidae, Ostraciidae, and a number of other Labridae (Taborsky 1994). Satellites appear to be reproductive competitors of bourgeois males in all of these cases, but nonetheless they are tolerated. Despite the great theoretical interest in individual relationships based on conflict and cooperation (Davies 1982; Seger 1991) and despite the widespread nature of this phenomenon in fishes (Taborsky 1994, 1999), none of the approximately 20 species described to date has been studied experimentally for the functional relationship between satellite and bourgeois males.

Pelvicachromis pulcher

This West African cichlid is polymorphic in the male sex. "Red morph males" reproduce either with a female in a monogamous pair or with several females in a harem. "Yellow morph males" may also become monogamous pair males, or they join the harem of a red morph male where they help defend the territory against reproductive competitors and predators of eggs and fry (Martin and Taborsky 1997). These satellites are fully tolerated in the territory of the harem owner and obtain a considerable share of fertilizations, so there is only a moderate reproductive skew in this cooperative breeding system. With the help of a genetic marker expressed in the color pattern of sons, it was shown that a monogamous pair male and the first satellite in the size hierarchy within a haremic territory sired a similar number of young, whereas harem owners sired nearly 3.5 times as many offspring. In comparison to dominant satellites, those in the second and third rank positions sired only about 50% and 16% of young, respectively (Martin and Taborsky 1997).

Despite the similar success of dominant satellites and pair males, the defense effort of satellite males against competitors and predators per sired young greatly surpassed that of pair males. Higher defense rates resulted in an increased risk of injury (Martin and Taborsky 1997). These results may indicate that the satellite tactic is chosen only if unpaired females or defendable breeding areas are not available to a male.

This breeding system is characterized by a high degree of reciprocity. Harem males tolerate satellites at the expense of reducing production of their own offspring due to intragroup reproductive competition between males. They gain, however, by the enormous defense effort of these helpers. The latter bear the costs of energetic investment and risk, but especially when dominant, they obtain a great share of the reproductive output within the territory. Satellites in the second or third rank positions expend more effort per success than dominant ones, but their competitive abilities are probably lower. They are in a waiting position for a better reproductive role as a dominant satellite or pair male, but still exploit reproductive opportunities within their group.

Neolamprologus brichardi/pulcher

This species is abundant along the rocky shores of Lake Tanganyika and belongs to a group of cichlids exhibiting the most highly developed social systems known among fish (Taborsky 1994). Young produced in a territory stay with the family usually long beyond sexual maturity (Taborsky 1984; Taborsky and Limberger

1981). Therefore reproductively mature helpers (both male and female) share the territory with a dominant pair of breeders. Occasionally female helpers may pair up with the male breeder and jointly expel the former female breeder from the territory or split off part of the female breeder's territory to form a harem (Taborsky 1985). Reproductive competition between male helpers and territory owners is much more prominent, with male helpers often participating when breeders spawn (Taborsky 1985). Based on genetic fingerprinting, these helpers were shown to sire about 10% of young in an experimental situation with a breeding pair and one or two mature male helpers (Dierkes et al. 1999).

In a population at Kasakalawe, Zambia, we found (using microsatellite markers) that nearly 80% of offspring produced in a territory were sired by the male territory owners, whereas the remaining young were probably sired by male helpers (Dierkes P, Taborsky M, and Achmann R, unpublished data). In principle, two mechanisms might explain why male breeders do not entirely monopolize reproduction within their territories. If breeders face the threat of helper departure, or helpers face the threat of being ejected (Johnstone 2000), then (1) breeders may provide male helpers with the opportunity to share in reproduction, as an incentive to stay (Johnstone et al. 1999; Keller and Reeve 1994; Vehrencamp 1983), or alternatively, (2) breeders may lack complete control of reproduction within their group (Cant 1998; Reeve et al. 1998; Taborsky 1985). In *N. brichardi/pulcher,* the latter applies. Male helpers act furtively when participating in the breeders' spawning, and they then face a high risk of eviction (Dierkes et al. 1999). In fact, helpers choose to stay in their natal territory even when provided with opportunities to breed independently (Taborsky 1985).

If reproductive competition occurs within *N. brichardi/pulcher* groups, why is there cooperation between competing group members? This question is particularly interesting with regard to the role of helpers in brood care and defense against predators of young, as both behaviors demand substantial energy investment (Grantner and Taborsky 1998; Taborsky and Grantner 1998) and the latter is additionally risky (Martin and Taborsky 1997). There are two ways that natural selection might favor such behavior: kin selection, if the offspring produced in the territory are related to helpers (Hamilton 1964), or reciprocity, when helpers "pay" for being allowed to stay in the territory (Gaston 1978; Taborsky 1984). The former possibility is rather unlikely to be important for large helpers of this species, as the degree of relatedness between helpers and beneficiaries declines with a helper's age (Taborsky and Limberger 1981). In fact, breeders in the Kasakalawe population are exchanged so often (due to high predation pressure) that relatedness is rather low between large, sexually mature helpers and the young produced by the territory owners (Dierkes P and Taborsky M, unpublished data). "Paying for staying" is probably the ultimate reason why large helpers of *N. brichardi/pulcher* behave cooperatively within their family groups (Taborsky 1984, 1985). By doing so, helpers increase the productivity of breeders, while themselves gaining protection against predation (Taborsky 1984). At Kasakalawe, removal experiments revealed that helpers also may benefit from territory inheritance if breeders disappear (Balshine-Earn et al. 1998).

Neolamprologus multifasciatus

This smallest of the cichlid species breeds in snail shells and between stones and rubble in Lake Tanganyika (Sato and Gashagaza 1997). Family groups in this species resemble those in *N. brichardi/pulcher,* with young staying with their parents beyond maturity and helping in territory defense and maintenance (especially sand digging; Kohler 1998). Sexually mature family members of both sexes attempt to participate in reproduction, and this may cause substantial fitness costs, especially for new male territory owners that have replaced the fathers of the mature helpers in the territory. Based on the data of Kohler (1998), the male territory owner was the genetic father of only 81.3% of the 91 offspring in 16 families that could be unequivocally attributed to a particular male (of interest, the same degree of multiple paternity as found in *N. brichardi/pulcher*). About 4.4% of the offspring were attributed to the largest male helper, while 14.3% of young had been sired by a male of unknown identity.

In contrast to the situation in *N. brichardi/pulcher,* females too regularly share in reproduction. In 9 of 18 analyzed groups containing offspring from two or more subsequent broods, young had been sired by two female group members, and in one case by three. On average, significantly more adult females than males were present per group (2.09 versus 1.44; $P < .001$; $z = 3.35$; $N = 45$ groups with adults of both sexes; based on data of Kohler 1998). At present, it is not known whether females suffer from reduced offspring production due to the reproductive participation of other female group members.

Why do reproductive competitors of both sexes in *N. multifasciatus* share a common territory and cooperate in its defense and maintenance? First, to a large extent these groups consist of relatives (Kohler 1998), so kin selection may be responsible for the cooperation found within families. Second, it may be difficult and risky for prospective dispersers to find a new territory, because this involves the energetic expense and danger of digging out shells and other shelters from beneath the sand (Kohler 1998). Therefore there may also be a reciprocal relationship among group members, with submissive members paying for their keep by participation in territorial and brood care duties. Third, there may be positive effects of group size on offspring production (present and future) and survival probabilities for both adults and offspring. In the closely related, cooperatively breeding cichlid *N. brichardi/pulcher,* more offspring were produced in larger groups, and workload decreased and feeding rate increased with group size (Balshine et al. 2001). If group size and synergistic effects from activities of group members have positive fitness consequences, mechanisms should persist ensuring that group members cooperate instead of parasitizing each other. Possible mechanisms are punishment by expulsion (Taborsky 1985), direct or indirect reciprocity (Nowak and Sigmund 1998; Trivers 1971) or effects of social prestige (Zahavi and Zahavi 1997).

Presently it is impossible to decide which of these three ultimate reasons (not mutually exclusive) are responsible for the cooperation found between reproductive competitors in *N. multifasciatus.* Although reproductive competition between group members occurs in both sexes, any fitness costs to females from reproductive competition within groups are probably not as high as those in males. For either sex, offspring production by other group members may result in space limitations and additional effort (e.g., in social interactions, brood care, defense), but in addition, the impeded fertilizations which accompany competition in the male sex are likely to result in the reduced production of an individual's own offspring.

Skew in Reproductive Investment and Success in Cooperative Groups

What can be learned from these four case studies of reproductive cooperation and competition within more or less "closed" reproductive groups or families? Usually competitors differ in dominance. That is, a bourgeois "resource owner" cooperates with submissive, sexually mature satellites or helpers of the same sex. Apart from dominance, these cooperative associations between reproductive competitors show varying degrees of asymmetries in investment and success (Taborsky 1999).

Skew in investment may reflect the quality and quantity of behaviors displayed. Defense behavior is shown by all submissive cooperators in the above examples. However, there are great differences with regard to who is attacked and the intensity of the attacks: either only conspecific reproductive parasites are attacked (*S. ocellatus*), or other conspecific competitors as well (*P. pulcher, N. brichardi/pulcher*), or heterospecific space competitors (*P. pulcher, N. brichardi/pulcher, N. multifasciatus*) and predators (*P. pulcher, N. brichardi/pulcher*). The quantity of defense behavior shown by satellites or helpers may exceed that of bourgeois territory owners (Martin and Taborsky 1997; Taborsky et al. 1986, 1987) or it may be much lower (Kohler 1998; Taborsky et al. 1986). Territory maintenance (e.g., digging in *N. brichardi/pulcher* and in *N. multifasciatus*) and brood care (*N. brichardi/pulcher*) may be shown by helpers as well, sometimes exceeding the effort of male territory owners (Taborsky and Grantner 1998).

The success of reproductive competitors appears always to be skewed strongly toward bourgeois males. However, in the two systems with unrelated satellite males, these appear to obtain a greater relative share than do the helpers in extended families. Dominant satellites obtain about 30% of the fertilizations in comparison to harem owners in *P. pulcher* (Martin and Taborsky 1997), and they show about 30% as many spawnings as nest owners in *S. ocellatus* (when summarized for an entire reproductive season; Taborsky M, Wirtz P, and Taborsky B, unpublished data). In contrast, in the family groups of *N. brichardi/pulcher* and *N. multifasciatus,* offspring sired by the largest male helpers made up only about 5–10% of the numbers produced by the respective territory owners (Dierkes et al. 1999; Kohler 1998).

What mechanisms are involved in the evolution of cooperative behavior between reproductive competitors? Fitness benefits to either party (bourgeois territory owners, and their satellites or helpers) may be reciprocal, or they may depend on relatedness. Reciprocal or mutual benefits appear to be involved in all described cases, either in the form of paying for permission to stay, or by synergistic effects of behavior that may depend on the number of individuals participating in activities such as territory defense. It is not clear whether effects of indirect reciprocity or prestige are involved as well. Kin selection may work in this context only when the cooperation increases production or survival of kin, so relatedness among the cooperating reproductive competitors must be above average and the cooperative behavior has to have positive fitness effects. Both conditions are met in *N. brichardi/pulcher* (Taborsky 1984; Taborsky and Limberger 1981). In *N. multifasciatus* families, relatedness is high, but increased production or survival of kin remains to be demonstrated (Kohler 1998).

The two possibilities illustrated above—reproductive competition involving cooperation between unrelated males or among members of extended families—may be more widespread in fish than is generally believed. In a recent literature review, published examples were found of 22 species (belonging to 10 families) in which satellites are tolerated by bourgeois males, and 8 species (in 2 taxonomic families) were uncovered with extended cooperative family groups (Taborsky 1994). Given how little is known about fish reproductive behavior, these are not small numbers.

The most unbiased sharing among reproductive competitors in fish is the joint spawning of male suckers (Catostomidae). In many species of this family, two males join a female, one on each side, and the trio spawns together with coordinated movements (e.g., Jenkins and Jenkins 1980; Page and Johnston 1990; Reighard 1920). The unparalleled, mutual tolerance of spawning males in these species appears to be cooperation between scramble competitors. A set of hypotheses has been suggested to explain this exceptional riddle of fish reproduction (Taborsky 1994), but as yet they remain untested.

The Importance of Molecular Genetics for Unveiling Reproductive and Social Patterns in Fishes

The application of enzyme electrophoresis and molecular genetic techniques has helped greatly to uncover the relative reproductive success rates of competing males (Chebanov et al. 1983; Colbourne et al. 1996; DeWoody et al. 1998, 2000; Dierkes et al. 1999; Jones et al. 1998; Maekawa and Onozato 1986; Martinez et al. 2000; Moran et al. 1996; Philipp and Gross 1994; Rico et al. 1992; see DeWoody and Avise 2001 for a review). These methods may help to identify factors affecting relative success rates of different types of males, such as body size (Hutchings and Myers 1988; Thomaz et al. 1997). Without protein or DNA assays, paternity estimates rely on measured spawning rates (Gross 1991; Reeves 1907; Warner and Lejeune 1985; Warner et al. 1975), which are crude measures at best. Only in exceptional cases are genetically based phenotypic markers likewise available for paternity estimates (Martin and Taborsky 1997).

With molecular methods, other aspects of reproduction can also be illuminated, such as the partitioning of clutches of individual females among different males, or egg stealing between neighboring males (Jones et al. 1998; Rico et al. 1992). Such behavioral features can be observed directly as well (Assem 1967; Morris 1952; Taborsky et al. 1987; Wootton 1971), but genetic methods extend our ability to examine these phenomena. Furthermore, only by application of genetic techniques can family composition be understood in species with prolonged associations between reproductively mature group members (Kohler 1998). This field is hitherto unexplored, yet may provide important insights into the selection mechanisms involved in the evolution of advanced sociality.

The application of molecular genetic tools to address questions of the evolution of reproductive and social patterns in fishes has only begun. It is not far-fetched to predict that this field will flourish in the near future, and that it will revolutionize our understanding of the evolution of ARTs and of the mechanisms operating in highly social reproductive groups. I expect that this will have an even more profound effect on the comprehension of reproduction and sociality in general than did the application of molecular genetic techniques to the study of mating patterns in birds and mammals. Reproductive patterns in birds, for example, are relatively uniform, with variation at the behavioral level being confined mainly to the degree of overt and inconspicuous polygamy in both sexes. In comparison, in fishes the variation of reproductive patterns and of apparent adaptations to reproductive competition is enormous (Breder and Rosen 1966; Taborsky 1994). Highly divergent reproductive patterns exist side by side even within species. A precondition for understanding how alternative behavioral and life-history tactics can coexist within a species is the knowledge of their relative fitnesses. This involves the disclosure of reproductive success, which can only be achieved economically and on a large scale by application of molecular genetic tools. Particularly in the male sex, there is hardly any alternative to reach this goal.

Another role for molecular genetic techniques in the ecological genetics of fishes concerns the question of reproductive isolation between neighboring groups and populations. Especially in lacustrine freshwater fishes such as cichlids in the great lakes of East Africa, this aspect is important for understanding behavioral issues related to speciation (Knight et al. 1998; Markert et al. 2001; Seehausen et al. 1999; Sturmbauer et al. 1997).

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